



Species-specific facilitation, ontogenetic shifts and consequences for plant community succession

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Keywords

Abiotic stress; Assembly rules; Benefactor; Community structure; Competition; Establishment; Niche; Plant succession; Restoration ecology; Semi-arid; Species-specific patterns

Nomenclature

Tropicos Database (<http://www.tropicos.org/>; accessed on 5 Oct 2014)

Received 21 October 2014

Accepted 26 November 2015

Co-ordinating Editor: Francisco Pugnaire

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Introduction

Facilitation by nurse plants is now widely recognized as an important mechanism in the structuring of plant communities. Because facilitation and competition occur simultaneously, a clear understanding of the mechanisms driving the balance between these contrasting forces needs further attention (Holmgren et al. 1997; Brooker et al. 2008). The balance between facilitation and competition can vary depending on environmental severity (Bertness & Callaway 1994) and species stress tolerance (Liancourt et al. 2005; Maestre et al. 2009). Further, interactions between nurse and beneficiary species might be species-specific, where different nurse species facilitate or compete with distinct sets of beneficiary species (Call-

Abstract

Aims: Our main aims are to test how: (1) different nurse species modulate the early establishment of multiple beneficiary species in a degraded area; (2) the intensity and direction of species-specific interactions between nurse and beneficiary species change during beneficiary ontogeny.

Location: A shrubby Caatinga forest at Petrolina, northeast Brazil, degraded by grazing and logging activities in recent decades.

Methods: We conducted a factorial multi-species experiment in which seeds and seedlings of five beneficiary species were sown in the presence and absence of three pioneer tree species. Beneficiary species performance was monitored for different ontogenetic stages.

Results: We found evidence of species-specific facilitation in which the intensity and outcome of the interactions between nurse and beneficiary species varied depending on species identity. Additionally, for most combinations of nurse and beneficiary species, ontogenetic shifts from positive to neutral or negative interactions were observed with increasing beneficiary age.

Conclusions: We provide experimental evidence that nurse and beneficiary species identity simultaneously influence the balance between facilitation and competition. Our results suggest that ontogenetic shifts may be a widespread phenomenon in semi-arid ecosystems. We discuss that a key mechanism explaining these findings is the match between what nurse species offer and what beneficiary species require in terms of resources and conditions. As a consequence, different nurse species tend to favour or inhibit unique sets of beneficiary species beneath their canopies. We argue that species-specific facilitation is an overlooked mechanism promoting β -diversity during community succession.

away 1998; Gómez-Aparicio et al. 2004). Mesquita et al. (2001) studied Amazonian secondary succession and showed that species-specific facilitation can strongly influence community succession. The authors reported that sites dominated mainly by the pioneer *Cecropia sciadophylla* developed denser communities with higher species richness and different composition when compared with sites dominated by the pioneer *Vismia guianensis*. This suggests that species-specific interactions can promote alternative successional pathways (Mesquita et al. 2001). However, the extent to which species-specific facilitation influences plant community succession requires further consideration.

In environments with severe abiotic stress, pioneer woody species often act as nurse plants, ameliorating

microclimatic conditions and enhancing soil nutrients (Flores & Jurado 2003). In open areas, nurse plants provide 'islands of fertility' where more favourable conditions for establishment occur (Pugnaire et al. 1996). Thus, facilitation by nurse plants play an important role in maintaining the diversity of harsh environments by increasing species richness at the community level (Hacker & Gaines 1997; Cavieres & Badano 2009; Cavieres et al. 2014). However, because different pioneer species can have contrasting effects beneath their canopies, species-specific patterns are likely to emerge. Several mechanisms may generate species-specific plant interactions, and they are linked to the variety of ways that nurse plants influence resources and conditions, such as soil water content, nutrient availability, microclimate and herbivore pressure (Callaway 1998). Landero & Valiente-Banuet (2010) found that the different effects of nurse plants on shade and soil nutrients might explain species-specific facilitation on the early performance of the endemic cactus *Neobuxbaumia mezcalensis*. The final outcome of plant–plant interactions between nurse and beneficiary species will also depend on the ecological strategy of the beneficiary species and how strongly it relies on the resources provided by nurses (Liancourt et al. 2005; Maestre et al. 2009).

Studies on plant spatial distribution have shown that, as beneficiary plants grow, ontogenetic shifts from facilitation to competition may emerge due to competition for water and other resources (Miriti 2006). For example, the shade from nurse plants can provide better microclimatic conditions for young individuals to establish under water stress (Franco & Nobel 1989), but shade and competition for soil resources can be an impediment to the growth of older beneficiary species (Reisman-Berman 2007). Miriti (2006) found strong ontogenetic shifts from facilitation to competition in neighbours of *Ambrosia dumosa*, which improved the performance of juveniles but competed with adults. Although many examples of ontogenetic shifts can be found in the literature (Rousset & Lepart 2000; Ganade & Brown 2002; Miriti 2006; Armas & Pugnaire 2009), controlled experiments can provide new insights into the factors driving plant–plant interaction shifts (Schiffers & Tielbörger 2006; Bullock 2009). To fully understand if ontogenetic shifts in nurse/beneficiary interactions depend on species identity, we need to implement factorial multi-species experiments comparing the development of different beneficiary species underneath the same nurse plant.

In degraded dry ecosystems, where open sites impose strong abiotic constraints to the establishment of new recruits, nurse plants play a central role for seedling regeneration dynamics and may enhance an ecosystem's resilience to disturbance (Holmgren & Scheffer 2001;

Flores & Jurado 2003). In these systems, pulses of resource availability, especially through inter-annual variations in rainfall, can greatly influence plant community regeneration (Kitzberger et al. 2000). While humid years offer a window of opportunity for seedling establishment in open sites, dry years can limit plant species' regeneration (Kitzberger et al. 2000; Holmgren & Scheffer 2001; Barchuk et al. 2005). In highly disturbed sites where native vegetation has been primarily removed, environmental harshness adds additional restrictions to plant colonization (e.g. bare soil, high temperatures and nutrient leaching), reducing the likelihood of natural recovery (Holmgren & Scheffer 2001). In this scenario, the use of nurse plants can be a key technique for managing degraded areas (Padilla & Pugnaire 2006). Understanding how nurse plants differ in the ways in which they affect different beneficiary species will be crucial for developing advanced restoration methods (Gómez-Aparicio et al. 2004).

This work aims to reveal experimental evidence for ontogenetic shifts and species-specific facilitation, proposing a framework to understand the consequences of such interactions for community succession. Our main aims are to test how: (1) different nurse species modulate the early establishment of multiple beneficiary species in a degraded area; (2) the intensity and direction of species-specific interactions between nurse and beneficiary species change during beneficiary ontogeny.

Methods

Study site

The study was conducted on a 0.5-ha site at the Centre for Restoration of Degraded Areas (CRAD) (9°19'45.10" S 40°32'52.44" W), located near Petrolina, northeastern Brazil. The climate is semi-arid and characterized by periodic severe droughts and a high variability of inter-annual rainfall (Prado 2003). The historical mean annual rainfall is 462 ± 202 mm (climatic data from 1962 to 2012; available at <http://www.inmet.gov.br>), with the rainy season occurring from Nov to Apr. The vegetation consists of a shrubby Caatinga forest that has been degraded by grazing and logging activities in recent decades. There are only 30 plant species currently growing at the site; 20 are annual herbs, and ten are woody species (unpubl data). The study site has been fenced since 2005 to avoid goat browsing. The low diversity of tree species found at the site is probably due to past disturbances, resulting in loss of vegetation cover and absence of seed sources from surrounding areas. The following woody plants are dominant in the area: *Mimosa tenuiflora* (Willd.) Poir. (Fabaceae), *Poincianella microphylla* (Mart. ex G. Don) L.P. Queiroz (Fabaceae), *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) and

Cnidocolus quercifolius Pohl (Euphorbiaceae) (unpubl data).

Study species

Based mostly on successional criteria, species selected for the study were classified into two groups: potential nurse plants (hereafter nurse plants) and beneficiary species. To select nurse species, the following criteria were required: (1) ability to colonize open sites and degraded areas (pioneers); (2) short periods of leaf deciduousness (to provide shade for longer periods); (3) woody species common in Caatinga; and (4) dominant tree species at the study site. There were only four tree species present at this degraded site, and the three species selected are the only ones that met all of the criteria described above. Nurse plants selected for the experiment were: *Cnidocolus quercifolius* Pohl (Euphorbiaceae), *Mimosa tenuiflora* (Willd.) Poir. (Fabaceae) and *Poincianella microphylla* (Mart. Ex G. Don) L.P. Queiroz (Fabaceae). Additionally, field evidence has shown that these three species might function as facilitators due to higher richness and abundance of regenerating plants below their canopies when compared to open areas (unpubl data). It is important to highlight that these three species show different canopy architecture, leaf size and nitrogen-fixing ability, which allows our study design to test the species-specific influence of nurses on beneficiary species.

Beneficiary species were selected based on the following criteria: (1) tree species from a later successional stage; (2) species common in Caatinga; (3) species with fast germination rates (a common feature for Caatinga trees); and (4) species available from local seed collection. Beneficiary species selected for the experiment were: *Amburana cearensis* (Allemão) A.C. Sm. (Fabaceae), *Aspidosperma pyrifolium* Mart. (Apocynaceae), *Erythrina velutina* Willd. (Fabaceae), *Myrcodruon urundeuva* Allemão (Anacardiaceae) and *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae). *P. pyramidalis* is the only beneficiary species that has the ability to establish in open areas, but it was still used in our study because it occurs quite frequently in pristine Caatinga forests. Beneficiary species differ in relation to their light demands for establishment, nitrogen-fixing ability and conservation status. In the seedling transplantation experiment, *A. cearensis* was not used due to the lack of available seedlings. Germination and establishment tests were conducted for seeds of all beneficiary species in a greenhouse located at CRAD. The seeds of all beneficiary species were able to germinate in the greenhouse experiments, and their germination rates were as follows: *A. pyrifolium* (17%), *M. urundeuva* (56%), *A. cearensis* (85%), *E. velutina* (86%) and *P. pyramidalis* (91%) (Appendix S1).

Multi-species field experiment

Seeds and seedlings of the five beneficiary species (*A. pyrifolium*, *M. urundeuva*, *A. cearensis*, *E. velutina* and *P. pyramidalis*) were placed in the field and subjected to the presence and absence of three nurse species (*Cnidocolus quercifolius*, *Mimosa tenuiflora* and *Poincianella microphylla*). The experiment was structured using a split-plot design, with 'nurse' and 'no nurse' treatments as a split factor. Eight adult individuals of each nurse species were selected randomly from a pool of all eligible individuals at the site. Nurses selected were usually surrounded by bare soil and had no crown overlap with neighbouring shrubs or trees. A 3 m × 3 m plot was delimited with each nurse plant individual at the centre, comprising an area of 9 m² under the selected plant (nurse treatment). For the no nurse treatment, paired 3 m × 3 m plots were randomly placed in open areas within a 7-m range from the nurse plants. In these areas, adult woody plants were absent, and ground was frequently bare. Pairs of plots with and without nurse plants were considered blocks and were located 2–40 m apart. Each 3 m × 3 m plot for nurse and no nurse treatments was divided into two subplots, each comprising half of the 3 m × 3 m plot area. In one subplot, groups of 25 seeds of each beneficiary species were randomly assigned into five quadrats (50 cm × 50 cm). Seeds were sown 10 cm apart and marked with wooden sticks. A total of 6000 seeds were used, 1200 per beneficiary species. In the opposite subplot, seedlings were randomly assigned into four quadrats (40 cm × 50 cm). Groups of four seedlings of each beneficiary species were transplanted (25 cm apart) inside each quadrat (with exception of *A. cearensis*, see above). A total of 768 seedlings (192 per beneficiary species) were used.

Experiments started in Jan 2010 at the beginning of the rainy season to improve germination and survival. Cumulative rainfall during the experimental period was only 177 mm (~50% lower than the historical average for the same period [338 mm]). This was one of the lowest precipitation levels in the region over the last 40 yr (see Appendix S2); therefore, our results represent an atypical dry year. Seeds were collected at local Caatinga sites and stored in a low-temperature chamber (5–7 °C) for approximately 6 mo, with the exception of *P. pyramidalis* seeds, which were stored for 2 yr. Mechanical scarification was applied to break *E. velutina* dormancy before the start of the experiment (Matheus et al. 2010). All seedlings were produced under identical conditions inside CRAD greenhouse and were 3–4 mo old. Before transplantation, seedlings were subject to full sun and limited water for 1 mo to simulate field conditions. All seedlings that died in the first week after transplantation were replaced.

For the seed sowing experiment, the number of seeds lost (predation, wind or run-off), the number of seeds germinated (root emergence) and the number of seedlings established (leaf emergence) were registered monthly over 5 mo. Repeated measures taken over the course of the experiment, for each measurement of seed performance, were summarized to produce the following response variables: total number of seeds lost, total number of seeds germinated and total number of seeds established.

To understand how different nurse species modulate the early establishment of multiple beneficiary species we used the response variables described above to run a split-plot generalized mixed model (GMM) with binomial error for each nurse species separately. We used binomial errors because our response variables are count data on proportions (Crawley 2012). Nurse effect treatment (nurse and no nurse) and beneficiary species treatment (five species) were used as explanatory fixed effects, while nurse effect within block was used as a random effect to account for the split-plot design (Crawley 2012). The significance of each fixed factor and interaction was tested with a log-likelihood ratio test (Crawley 2012). We used a GMM approach because our model contains both fixed and random effects.

To understand how the intensity and direction of the species-specific interactions between nurse and beneficiary species change during beneficiary ontogeny, we used data from the seed sowing and the seedling transplantation experiment to deal with a range of ontogenetic stages. To determine the intensity and direction of the interactions between each nurse and beneficiary species combination, the relative intensity index (RII; see Armas et al. 2004) was calculated for each of the following ontogenetic phases: seed survival, germination, establishment and seedling growth. The RII for seed survival, germination and establishment was calculated based on the seed experiment data. The RII for the germination and establishment phases was calculated considering only seeds that escaped predation and run-off. Seedling growth data was obtained from the seedling transplant experiment and represented the maximum growth registered (final minus initial height) between the four seedlings planted in a quadrat, over a 5-mo period. The RII is calculated from the formula:

$$\text{RII} = \frac{\text{Bw} - \text{Bo}}{\text{Bw} + \text{Bo}}$$

where (Bw) is the performance of the beneficiary species in the presence of nurse plants and (Bo) is the performance of the beneficiary species in the absence of nurse plants. This index represents the relative effect of nurse plants on

beneficiary species, varying from -1 (maximum competition) to $+1$ (maximum facilitation) (Armas et al. 2004).

We ran a linear model with the RII as a response variable and nurse species, beneficiary species and beneficiary ontogeny and their interactions as explanatory factors. Beneficiary ontogeny was included in the model as a categorical factor with four levels: seed survival, seed germination, seed establishment and seedling growth (see details above). To account for the spatial structure of the experimental design, nurse tree was used as an error term in the model to test for the nurse species effect. Although RII values are bounded between -1 and 1 , this index has well known statistical properties and its distribution is approximately normal (Armas et al. 2004). Detailed analysis of our model residuals revealed no trend (see Appendix S3), therefore we used a linear model instead of a generalized linear model for simplicity.

All statistical analyses were performed using R 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria; <https://www.R-project.org/>). GMMs were performed using the R lme4 package.

Results

Multi-species experiments

In general, nurse plants have no statistical effect on seed loss, with the exception of *P. microphylla*, which showed a significant interaction between nurse effect and beneficiary species, indicating species-specific interactions (Fig. 1b; $\chi^2 = 9.9$, $P = 0.042$; see Appendix S4 for details). Beneficiary species had different probabilities of seed loss. For instance, *M. urundeuva* and *E. velutina* had the highest rates, while other species showed probabilities equal to or lower than 20% (Fig. 1a–c).

The presence of nurse plants had a strong positive effect on seed germination probability for all beneficiary species, increasing germination from two- to nine-fold, depending on the identity of the beneficiary and nurse species (Fig. 1d–f, Appendix S4). For the nurse *C. quercifolius*, there was a significant interaction between nurse effect and beneficiary species, demonstrating that beneficiary species differed in the magnitude by which their germination performance was positively affected by this nurse ($\chi^2 = 11.3$, $P = 0.022$; Appendix S4). For instance, *A. cearensis* showed proportionately larger seed germination improvements when compared with other species (Fig. 1d). The presence of nurse plants also had positive effects on the seedling establishment of beneficiary species (marginal for *P. microphylla*) (Fig. 1g–i, Appendix S4). Although nurse plants improved the early performance of beneficiary species, all experimental plants (6000 seeds and 768 seedlings) died within 6 mo due to severe drought.

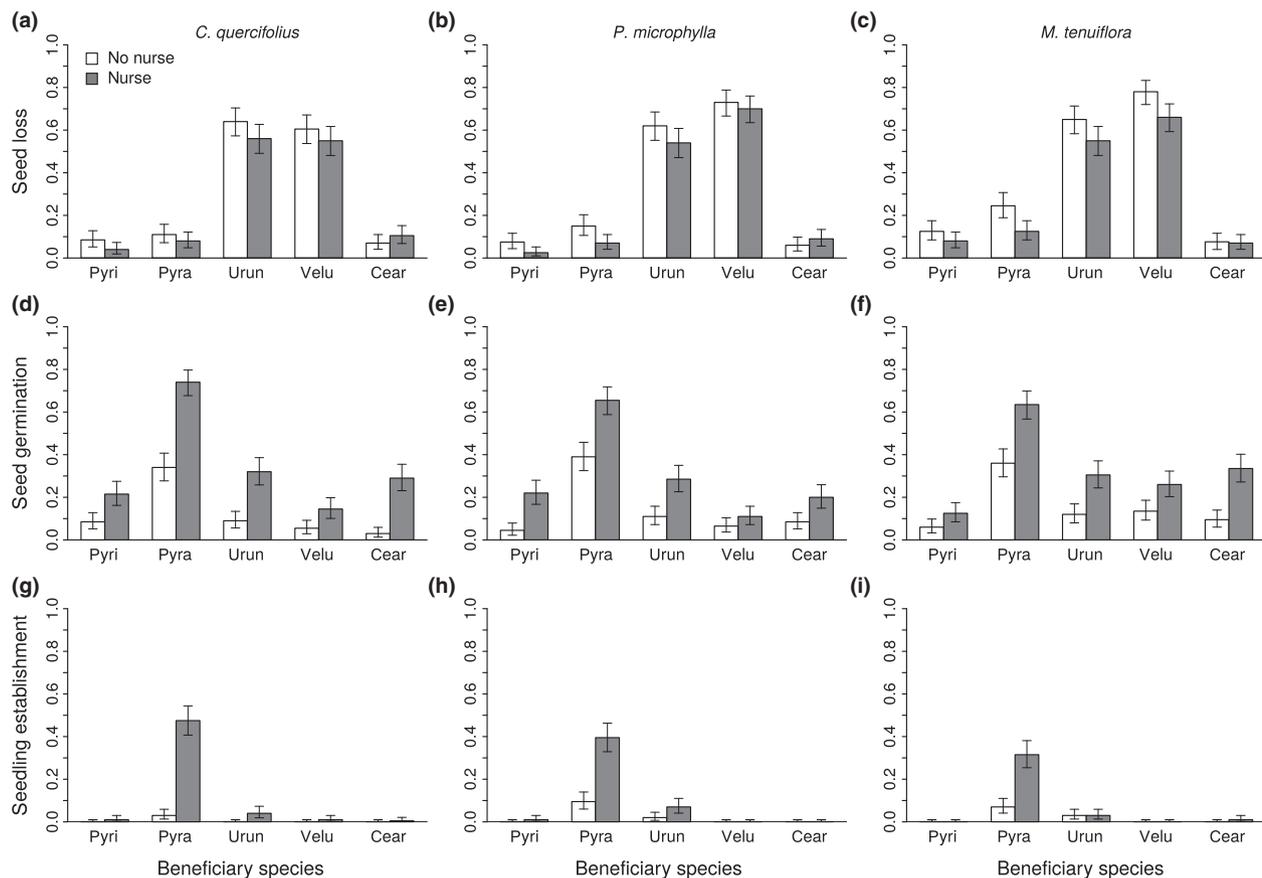


Fig. 1. Proportion of seed loss (a, b, c), seed germination (d, e, f) and seed establishment (g, h, i) for each nurse and target species. In the figure axes, pyri, pyra, urun, velu and cear represent *A. pyrifolium*, *P. pyramidalis*, *M. urundeuva*, *E. velutina* and *A. cearensis*, respectively. Error bars represent 95% confidence intervals.

Species-specific ontogenetic shifts

We found strong experimental evidence of species-specific interactions between nurse and beneficiary species, with the direction and intensity of interactions varying considerably between nurse/beneficiary pairs (Fig. 2; see Appendix S5 for details). Most interactions between nurse and beneficiary species were dominated by facilitation, especially during germination and establishment, when facilitation intensity was much higher (Fig. 2). For the majority of beneficiary species, the positive effects tended to decrease during the seedling growth phase and were neutral or slightly positive during the seed survival phase (Fig. 2). Negative interactions occurred only in one nurse/beneficiary combination (Fig. 2f), whereas *M. urundeuva* (a threatened species) was positively affected during all its ontogenetic phases by the nurse *M. microphylla* (Fig. 2h).

A significant interaction between nurse species and beneficiary species treatments demonstrates a species-specific pattern ($F = 2.1$, $P = 0.050$, Appendix S5), where some

nurses proved to be better for specific beneficiary species but showed neutral or negative effects for others. For example, the *C. quercifolius* nurse showed strong positive effects on *P. pyramidalis*, *A. pyrifolium* and *M. urundeuva* (Fig. 2a,d,g) but in general showed neutral effects on *E. velutina* (Fig. 2j). Interaction between nurse species and beneficiary ontogeny demonstrates that nurse species affects beneficiaries differently depending on their ontogeny ($F = 3.5$, $P = 0.002$, Appendix S5). For example, while *M. tenuiflora* showed a small positive effect on most beneficiary species in the establishment phase, *P. microphylla* and *C. quercifolius* showed much stronger effects, with *C. quercifolius* being the nurse species with the most consistent positive effect for this ontogenetic phase (Fig. 2). *M. tenuiflora* had a stronger positive effect on the seed survival phase for most beneficiary species when compared to other nurses, which generally showed neutral effects (Fig. 2i,m).

Finally, interaction between beneficiary species and beneficiary ontogeny show that the positive effect of nurse plants not only differed between beneficiary species, but

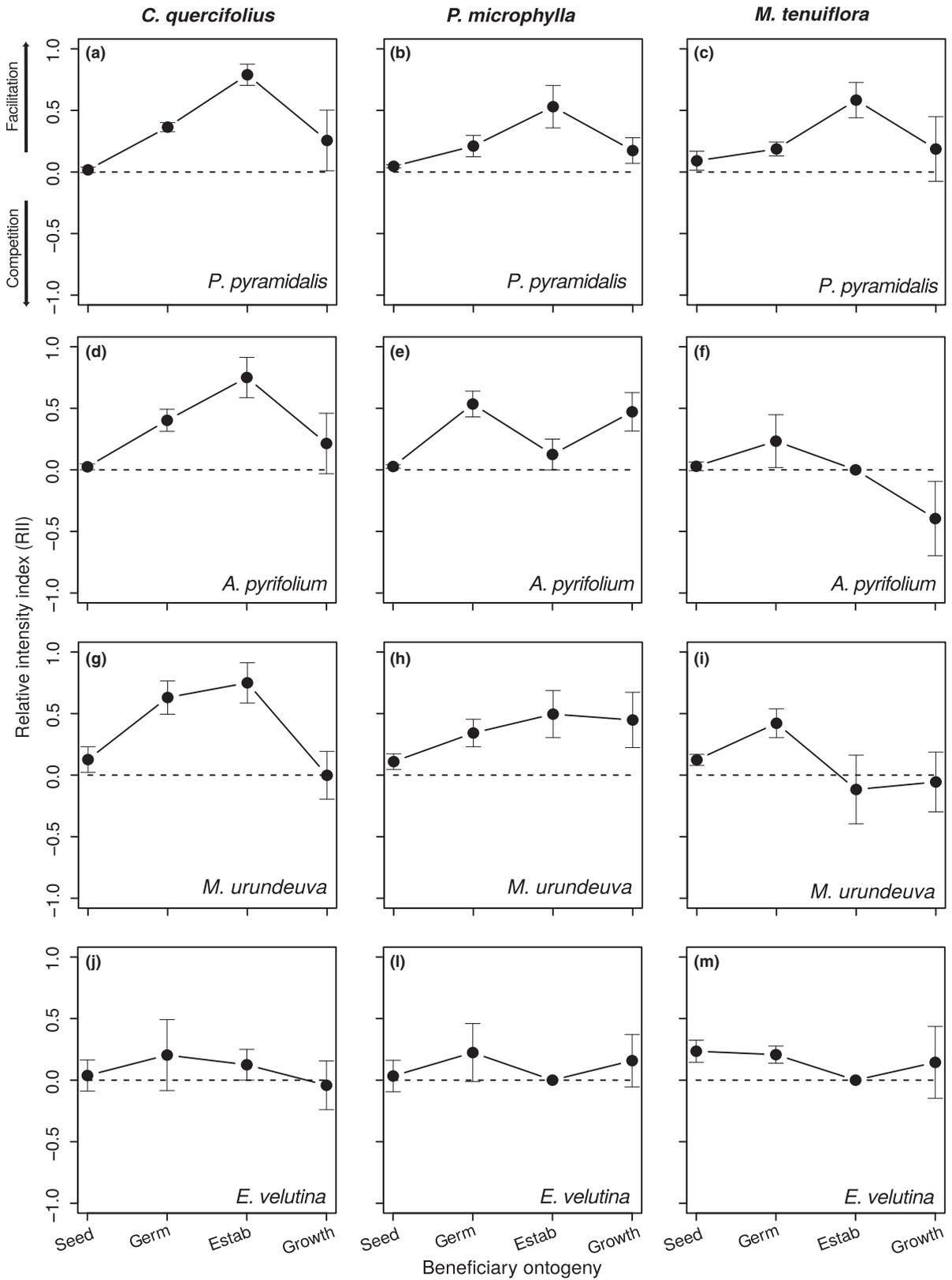


Fig. 2. Relative intensity index (RII) for each nurse/beneficiary combination during the following ontogenetic phases: seed survival (seed), seed germination (germ), seed establishment (estab) and seedling growth (growth). Error bars represent ±1 SE.

was also inconsistent in beneficiary species ontogeny ($F = 2.1$, $P = 0.026$, Appendix S5). For example, while the mean RII for the establishment phase was positive and very high for *P. pyramidalis*, it was not as high for *A. pyriformis* or *M. urundeuva* and was neutral for *E. velutina*. Overall, facilitation was more intense for *P. pyramidalis* and *A. pyriformis*, while nurse plants showed less positive or neutral effects on *E. velutina*.

Discussion

This study reveals that the balance between facilitation and competition can be simultaneously influenced by nurse and beneficiary identity as well as beneficiary ontogeny. For seed germination, all nurse species showed strong facilitation. However, as ontogenetic development progressed, differences between nurse plants became clear. *Poincianella microphylla* remained a good benefactor for improving beneficiary species' growth, while *C. quercifolius* and *M. tenuiflora*, depending on the beneficiary species in question, showed neutral or negative effects. These results indicate that plant community regeneration may be governed by species-specific facilitation where different pioneer species facilitate or compete with different sets of beneficiary species (Callaway 1998; Landero & Valiente-Banuet 2010). Our results reinforce the importance of performing multi-species experiments at the community level to reveal species-specific patterns (Brooker et al. 2008).

Mechanisms underlying species-specific interactions

Niche strategies are important mechanisms modulating species interactions. Vannette & Fukami (2014) proposed that species' niches can be decomposed into three components: (1) impact niche, which represents the way species alter environmental resources and conditions; (2) requirement niche, which represents the way species are dependent on particular resources and conditions for growth and survival; and (3) niche overlap, which represents similarities in the way interacting species use particular resources. We argue that this framework helps to explain the outcome of interactions between nurse and beneficiary species. The interaction net effect will depend on the match between the nurse species impact niche and the beneficiary species requirement niche. We expect strong inhibition by nurse plants when beneficiary species meet nurses with similar resource use (strong niche overlap; Valiente-Banuet & Verdú 2008; Verdú et al. 2012) or when the nurse impact niche worsens conditions required by beneficiary species (Holmgren et al. 1997). A neutral effect is expected when beneficiary species meet nurses that do not alter limiting resources or conditions required for beneficiary growth and survival. Finally, strong facilitation is

expected when nurse plants increase resources and/or improve conditions that match beneficiary' requirement niche (Vannette & Fukami 2014). This is more likely to occur when nurse and beneficiary species are not closely related (low niche overlap; Valiente-Banuet & Verdú 2008; Verdú et al. 2012) or beneficiary species are sensitive to environmental stress (Liancourt et al. 2005). Because differences in requirement niche and impact niche are frequently seen in the literature (Liancourt et al. 2005; Landero & Valiente-Banuet 2010), we predict that species-specific interactions are a widespread phenomenon across different types of ecosystems (Callaway 1998; Gómez-Aparicio et al. 2004).

Niche mechanisms can also help to elucidate inconsistencies related to the Stress Gradient Hypothesis (Bertness & Callaway 1994; Callaway & Walker 1997), such as unexpected facilitation in the wet tropics (Ganade & Brown 2002; Zanini et al. 2006) as well as nurse/beneficiary competition in extremely dry areas (Maestre & Cortina 2004). Competition might occur in stressful environments when nurse species do not match beneficiary species' needs, while facilitation might occur in productive environments when nurse species match beneficiary species' needs.

Ontogenetic shifts

Ontogenetic shifts from facilitation to competition are a common phenomenon when nurse and beneficiary species interact (Miriti 2006; Armas & Pugnaire 2009). However, the influence of species identity on ontogenetic shifts remains little explored and difficult to predict. We propose that the inclusion of the ontogenetic niche (Werner & Gilliam 1984) into Vannette & Fukami (2014) framework can shed light on the mechanisms generating complex species-specific interactions along ontogeny, such as those found in this study. Interaction shifts are more probable to be caused by ontogenetic changes in the requirement niche of beneficiary species. This is because mature nurse individuals are less likely to vary the way they alter resources and conditions through time. Ontogenetic shifts from positive to negative interactions are expected to occur when niche overlap increases as beneficiary species become larger and require more resources (Miriti 2006). An interesting illustration of this mechanism was reported by Nuñez et al. (2009), where shelter provided by shrubs had a positive effect on small individuals of *Austrocedrus chilensis* while medium-height individuals experienced water competition and larger individuals were not affected. The authors argued that this might be explained by the degree of niche overlap in root depth during *A. chilensis* ontogeny (Nuñez et al. 2009). Ontogenetic shifts from positive to neutral can occur when niche overlap decreases with ontogeny and beneficiary species become less dependent

on the resources or conditions provided by nurses. Indeed, we found many situations where the interaction balance tends to follow this trajectory. For example, *M. urundeuva* under *M. tenuiflora* was facilitated in the seed and germination phases but was not affected in later ontogenetic stages. These results reinforce the role of pioneer trees for the early establishment of late successional species in dry ecosystems (Gómez-Aparicio et al. 2004).

Finally, it is important to highlight that in some situations, beneficiary species might rely on complex combinations of resources and conditions. For example, if a nurse plant increases soil water content (a limiting resource in arid ecosystems) but does not provide light conditions that match beneficiary needs, the net nurse effect can be neutral since beneficiary species seedlings strongly depend on the right combination of water and light (Holmgren et al. 1997). Alternatively, a different nurse plant that improves soil water content and provides adequate light conditions will have a net positive effect. Additionally, part of the net nurse effect on the beneficiary might be linked to indirect facilitation through understorey species (Levine 1999), we believe that this process had a minor impact on our study since the regenerating community beneath nurse plants was quite sparse and variable between replicates (unpubl data).

Species-specific facilitation and community succession

The fact that facilitation intensity can be species-specific brings a new perspective to how plant communities develop during succession. In this scenario, beneficiary species might have unequal likelihood of survival beneath different nurse species. As a result, beneficiary species will

tend to be spatially associated with their preferred nurse plants (Fig. 3). Therefore, plant communities with low pioneer richness will maintain low species richness during succession (assuming that individual density and average facilitation effect of different nurse species are similar). In extreme cases where a single pioneer nurse species dominates succession, beneficiary species that experience facilitation under this particular nurse might spread, leading to alternative successional pathways depending on the identity of the dominant nurse plant (Mesquita et al. 2001). It is important to notice that when dominant pioneer species impose strong inhibition on late colonizers it prevents the successional sequence from continuing (Connell & Slatyer 1977). Alternatively, plant communities with a high diversity of pioneers would tend to maintain not only higher species richness but also higher β -diversity because multiple nurse species can favour different sets of beneficiaries (Fig. 3). Recent evidence suggests that different nurse plants might generate vegetation patches with a distinct understorey composition (Verdú et al. 2010), especially when pioneers species are phylogenetically unrelated (Valiente-Banuet & Verdú 2007; Verdú et al. 2012). The predictions described above can be tested by comparing the β -diversity of a regenerating community beneath nurse patches with contrasting pioneer species identity, richness and phylogenetic distance.

Implications for restoration ecology

Nurse plants are now widely recognized as tools for restorations programmes (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). Our results indicate that pioneer trees are good candidates for ecological restoration in Caa-

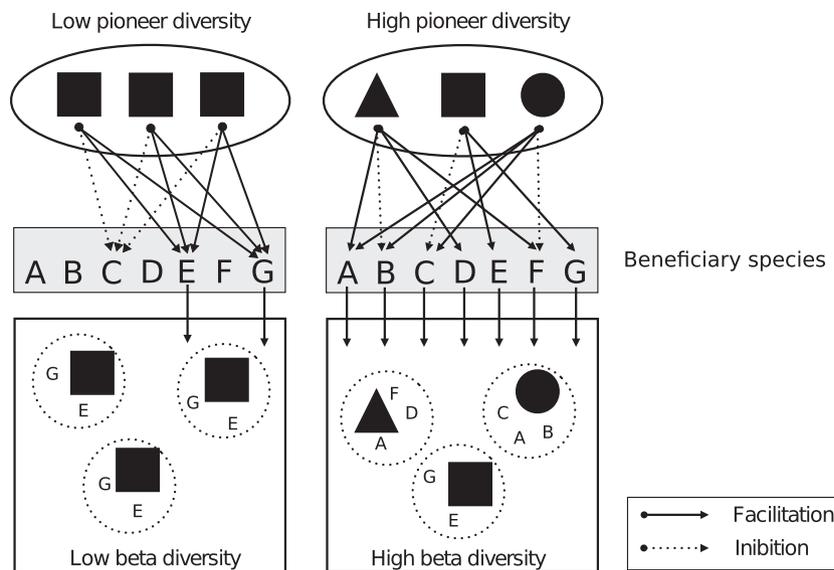


Fig. 3. Theoretical framework predicting the consequences of species-specific facilitation on community β -diversity during succession.

tinga because they favour the establishment of late successional species in the system (Clements 1916; Gómez-Aparicio et al. 2004). Previous vegetation survey beneath the nurse plants used in this study showed that some endemic and endangered species were only found regenerating below their canopies (unpubl data). Therefore, the use of nurse trees in restoration projects might also help to recover local diversity of degraded areas in dry ecosystems (Zonneveld et al. 2012; Hacker & Gaines 1997; Gómez-Aparicio et al. 2004). A fine-scale understanding of how species-specific interactions affect regeneration dynamics could refine nurse-assisted techniques and provide direct insights into which nurse/beneficiary combinations should be used to improve the likelihood of plant survival during restoration (Padilla & Pugnaire 2006; Gómez-Aparicio 2009; Verdú et al. 2012).

Conclusions

This work highlights that nurse and beneficiary species identity simultaneously influence the balance between facilitation and competition. We suggest that the match between what nurse plants offer and what beneficiary species require through ontogeny is a key mechanism to understand shifts in plant–plant interactions. Studies on nurse and beneficiary niche requirements could improve our capability to predict which plant species would function as the most suitable nurse for a given beneficiary for restoration purposes. Given that nurse species might favour different sets of beneficiary species beneath their canopies (Verdú et al. 2010), future works might test how richness of pioneer species influence β -diversity during community succession in degraded areas.

Acknowledgements

We are grateful to F. Basso, A. Kimber and J. Guedes for help with the fieldwork. We thank CRAD-Univasf for logistic support. This study was funded by Conselho Nacional de Pesquisa e Tecnologia (CNPQ), which provided grants to G.B. Paterno and G. Ganade (PQ/Produtividade). We thank G. Mazzochini for statistical support and T. Conradi, C.R. Fonseca, J. L. Attayde, G. Costa, A. Fadigas, C.C. Toledo, D.L. Rohr, A. Davidson and K. Wolcott for important comments on this manuscript. We also thank three anonymous reviewers for their insightful suggestions on an earlier version of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Greenhouse tests for seed germination and establishment for all beneficiary species.

Appendix S2. Histogram of historical precipitation (mm) during experimental months from 1962–2012. Red line represents the precipitation during the experimental year.

Appendix S3. Residuals analysis for the linear model of the Relative Intensity Index (RII).

Appendix S4. Table with results of a split-plot GMM with binomial family distribution for seed loss, seed germination and seedling establishment of each nurse species.

Appendix S5. Table with results of a linear model for the RII as response variable and nurse species, beneficiary species and beneficiary ontogeny as explanatory variables.